

THE AVIAN EGG: WATER VAPOR CONDUCTANCE, SHELL THICKNESS, AND FUNCTIONAL PORE AREA

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Gas exchange in the avian embryo has been shown to be dependent on, and limited by, the diffusive properties of gases across the resistance offered by the shell and shell membranes (Wangensteen and Rahn 1970-71). For simplicity, we shall use the term "shell" to denote the entire barrier to diffusion between the interior of the egg and the environment. It has also been shown that under normal conditions the diffusion of water vapor across the egg shell approximates the diffusion equations set forth for ideal gases (Paganelli et al. 1971) and that the weight loss in eggs is almost entirely due to diffusion of water through the shell (Romanoff and Romanoff 1949). The diffusive rate of water loss from eggs is:

$$\dot{V}_{\text{H}_2\text{O}} = K_{\text{H}_2\text{O}} \cdot A \cdot \Delta P_{\text{H}_2\text{O}} \quad (1)$$

where

$$\dot{V}_{\text{H}_2\text{O}} = \text{diffusive rate of water loss (cm}^3 \text{ STP} \cdot \text{sec}^{-1}\text{)}$$

$$K_{\text{H}_2\text{O}} = \text{permeability constant of the shell (cm}^3 \text{ STP} \cdot \text{cm}^{-2} \cdot \text{torr}^{-1} \cdot \text{sec}^{-1}\text{)}$$

$$A = \text{surface area of the shell (cm}^2\text{)}$$

$$\Delta P_{\text{H}_2\text{O}} = \text{water vapor pressure difference across the shell (torr)}$$

In our attempt to compare the rate of water loss among different species, it is useful to change the dimensions of Eq. (1) so that the volume of water vapor is expressed as a mass unit and to introduce the term water vapor conductance, which by definition is the product of the first two terms ($K_{\text{H}_2\text{O}} \cdot A$) (Rahn et al. 1971; Piiper et al. 1971) and which furthermore does not require measurement of surface area. Thus, the water vapor conductance of an egg shell is:

$$G_{\text{H}_2\text{O}} = \frac{\dot{M}_{\text{H}_2\text{O}}}{\Delta P_{\text{H}_2\text{O}}} \quad (2)$$

where

$$G_{\text{H}_2\text{O}} = \text{water vapor conductance (mg} \cdot \text{day}^{-1} \cdot \text{torr}^{-1}\text{)}$$

$$\dot{M}_{\text{H}_2\text{O}} = \text{the rate of weight loss (mg} \cdot \text{day}^{-1}\text{)}$$

$\Delta P_{\text{H}_2\text{O}}$ = water vapor pressure difference across the shell (torr)

We now have two ways of expressing the rate of water loss from an egg: either as water vapor *permeability*, $K_{\text{H}_2\text{O}}$, which is useful in comparing the differences that exist within a species; or as water vapor *conductance*, $G_{\text{H}_2\text{O}}$, which is useful for comparisons among species. Some authors have used the term *porosity* instead and have given various operational definitions and arbitrary conditions or units to define it (e.g., Mueller and Scott 1940; Tyler 1945; Romanoff and Romanoff 1949; Mueller 1958; Marshall and Cruikshank 1938).

On the assumption of diffusive flux for water vapor, we have attempted to set up standards to describe the "porosity" of the avian egg shell. We believe that for our comparative study this is best described as *conductance to water vapor* under standard conditions. Only under such conditions can values be compared when determined at different barometric pressures and temperatures.

In this study we have measured the water vapor conductances of fresh eggs of 29 species and shown how this value increases with egg weight. The change in egg shell thickness with egg weight has also been determined from data available in the literature (Schönwetter 1960-71). We have used these two relations to predict the total functional pore area in the egg shells of birds.

MATERIALS AND METHODS

DETERMINATION OF WATER VAPOR CONDUCTANCE

This was done by measuring periodically the rate of weight loss of eggs under known conditions of temperature, humidity, and barometric pressure. Fresh eggs from different species were brought to the laboratory and their initial weights were recorded (table 1). The eggs were placed in covered desiccators above dry, fused KOH pellets, which maintained the humidity close to zero. The desiccators were vented to room air through a short, KOH-filled column to assure pressure equilibrium and held at a constant temperature of either $20 \pm 1^\circ\text{C}$ or $25 \pm 1^\circ\text{C}$. Such temperatures do not permit development of the avian embryo (Funk and Biellier 1944). Once a day, the desiccators were opened, the eggs quickly weighed,

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TABLE 1. Standard water vapor conductance values, initial egg weights.

Species	No. of eggs	Initial egg wt. g \pm SD	Water conductance (mg \cdot day ⁻¹ torr ⁻¹)
<i>Troglodytes aedon</i> (House Wren)	27	1.32 \pm 0.130	0.65 \pm 0.428
<i>Dendroica petechia</i> (Yellow Warbler)	3	1.60 \pm 0.086	0.45 \pm 0.308
<i>Iridoprocne bicolor</i> (Tree Swallow)	5	1.72 \pm 0.067	0.50 \pm 0.049
<i>Passer domesticus</i> (House Sparrow)	21	2.62 \pm 0.148	0.88 \pm 0.334
<i>Molothrus ater</i> (Brown-headed Cowbird)	7	3.33 \pm 0.404	1.00 \pm 0.363
<i>Agelaius phoeniceus</i> (Red-winged Blackbird)	18	3.59 \pm 0.390	1.73 \pm 0.615
<i>Quiscalus quiscula</i> (Common Grackle)	3	6.29 \pm 0.032	2.98 \pm 0.955
<i>Turdus migratorius</i> (American Robin)	6	6.46 \pm 0.084	1.42 \pm 0.280
<i>Coturnix coturnix</i> (Japanese Quail)	12	9.62 \pm 0.660	3.09 \pm 0.700
<i>Pluvialis apricaria</i> (Eurasian Golden Plover) ^a	3	32.64 \pm 0.051	5.02 \pm 4.714
<i>Phasianus colchicus</i> (Ring-necked Pheasant)	12	33.84 \pm 2.338	6.60 \pm 0.847
<i>Lophura nyctheorus</i> (Chinese Silver Pheasant)	3	39.94 \pm 0.981	9.27 \pm 0.672
<i>Haematopus ostralegus</i> (European Oystercatcher) ^a	2	41.45 \pm 0.401	6.80 \pm 0.186
<i>Phalacrocorax auritus</i> (Double-crested Cormorant) ^b	8	49.88 \pm 3.372	5.56 \pm 3.172
<i>Numenius phaeopus</i> (Whimbrel) ^a	4	53.46 \pm 0.403	9.74 \pm 1.494
<i>Gallus gallus</i> (Domestic Chicken)	12	53.89 \pm 2.134	14.36 \pm 2.375
<i>Fratercula arctica</i> (Common Puffin) ^a	6	59.65 \pm 3.430	7.99 \pm 1.229
<i>Larus canus</i> (Mew Gull) ^a	8	76.20 \pm 4.476	15.01 \pm 2.859
<i>Cairina moschata</i> (Muscovy Duck)	4	80.20 \pm 7.610	12.32 \pm 0.983
<i>Anas boscas</i> (Pekin Duck)	11	82.34 \pm 5.610	14.47 \pm 1.536
<i>Larus fuscus</i> (Lesser Black-backed Gull) ^a	6	84.90 \pm 4.275	16.03 \pm 1.641
<i>Meleagris gallopavo</i> (Turkey)	11	87.76 \pm 4.317	13.49 \pm 1.258
<i>Larus argentatus</i> (Herring Gull) ^b	3	88.16 \pm 3.974	16.54 \pm 1.932
<i>Catharacta skua</i> (Great Skua) ^a	6	95.47 \pm 5.410	18.42 \pm 0.307
<i>Larus marinus</i> (Great Black-backed Gull) ^a	9	110.80 \pm 12.074	16.74 \pm 2.665
<i>Anser domesticus</i> (Emden Goose)	11	170.21 \pm 10.001	27.71 \pm 4.300
<i>Dromiceius novaehollandiae</i> (Emu) ^c	1	577.62	51.83 \pm 1.713
<i>Rhea americana</i> (Rhea) ^c	2	609.26 \pm 80.865	77.69 \pm 16.950
<i>Struthio camelus</i> (Ostrich) ^c	1	1480.03	104.76 \pm 4.263

Values and their standard deviations are listed in an increasing order of egg weights. Footnotes indicate geographical origin or source of egg: a = Faeroe Islands, Denmark, N.E. Atlantic; b = Mt. Desert Island, Maine; c = San Diego Biological Gardens. Absence of footnotes indicates that eggs were from Buffalo, N.Y. area.

the KOH pellets stirred, and actual weighing time, temperature, and barometric pressure recorded. Each experiment lasted 7–9 days. Eggs that did not have a steady rate of weight loss or showed an abnormally high rate of weight loss were checked for cracks and discarded if the shells were found to be defective.

CALCULATIONS

Weight loss was expressed as water loss per 24 hr, and corrected to a standard barometric pressure of 760 torr, since the rate of diffusion is inversely proportional to the total pressure. Paganelli et al. (1971) demonstrated that this is true for water loss across the egg shell. The corrected value was then divided by the water vapor pressure difference across the shell. Since the desiccator atmosphere has essentially zero humidity, the water vapor pressure difference was assumed to be equal to the water vapor pressure of saturation at the egg temperature. For our purpose, the very small reduction of vapor tension caused by the solutes of the egg contents can be neglected.

The result was not corrected further to a given temperature since evaporation from eggs per unit of water vapor pressure difference is not sensitive to temperature in the range of normal biological temperatures (Smith 1930, 1933; Ar and Paganelli, unpubl. data).

RESULTS AND DISCUSSION

Experiments were performed on different numbers of eggs (1–27) from 29 species. Six

to eight measurements were obtained from each egg and all the values for a given species averaged. The results are summarized in table 1.

Romanoff and Romanoff (1949) describe the daily water loss of 10–100 g eggs under constant conditions (not specified) as a linear function of the initial egg weight. These observations were made on 10 domestic and semidomestic fowls. We have extended the measurements to egg weights over three orders of magnitude in 29 species of altricial and precocial birds. A relation between G_{H_2O} and W , the fresh egg weight in grams, was derived from a linear regression analysis of $\log G$ on $\log W$ (fig. 1). It can be expressed as the following power function:

$$G_{H_2O} = 0.432 \cdot W^{0.780} \quad (3)$$

or in log form:

$$\log G_{H_2O} = -0.3645 + 0.780 \cdot \log W \quad (\pm 0.104 \text{ SE of estimate})$$

The correlation coefficient is high ($r = 0.986$) and significant ($P \ll 0.001$).

Since the conductance of the whole egg in-

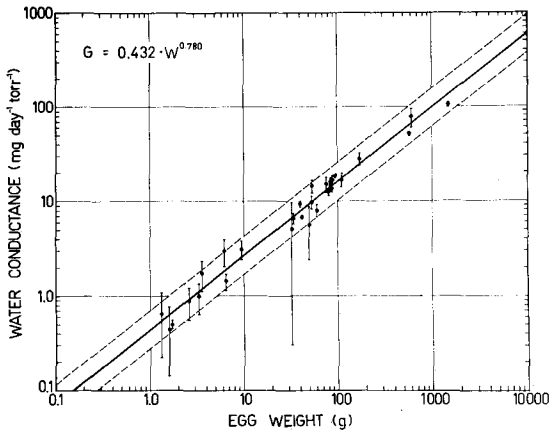


FIGURE 1. Regression of egg shell water vapor conductance (G) on the initial weight (W) of egg. Points represent grand means. Vertical bars indicate \pm standard deviations. The dotted lines enclose ± 2 standard errors of estimate, and represent the 95% confidence limits for the log of conductance.

creases with egg weight raised to a power less than 1.00, it means that the rate of water loss per gram egg weight decreases as the eggs get larger; in other words, large eggs can save more water than small eggs. Both Needham (1931) and Romanoff and Romanoff (1949) noted that species with large eggs tend to have longer incubation periods and thus would be exposed longer to water losses. This problem is discussed in detail by Rahn and Ar (1974) who showed that the extended incubation period in larger eggs is compensated for perfectly by the reduction in water vapor conductance per unit egg weight which they express as a common water loss coefficient for all eggs.

THE RELATIONSHIP BETWEEN CONDUCTANCE AND FICK'S LAW OF DIFFUSION

By definition, the conductance G_x is the flux across the shell per unit of gas tension difference, ΔP_x , across the shell, as shown for water vapor in Eq. (2). On the assumption that this flux is by diffusion through the pores of the shell only and that we have a steady state of flux, Fick's first law of diffusion can be modified (Wangensteen et al. 1970-71) so that water vapor flux is expressed as follows:

$$\dot{M}_{\text{H}_2\text{O}} = c \cdot D_{\text{H}_2\text{O}} \cdot \frac{A_p}{L} \cdot \Delta P_{\text{H}_2\text{O}} \quad (4)$$

where the new symbols are:

$$D_{\text{H}_2\text{O}} = \text{diffusion coefficient of water vapor in air (cm}^2 \cdot \text{sec}^{-1}\text{)}$$

$$A_p = \text{total functional pore area (cm}^2\text{)}$$

L = length of pores or shell thickness (cm)

c = conversion constant, $155.52 \cdot 10^7 / (R \cdot T)$ where the numerator has the units of $\text{sec} \cdot \text{mg} \cdot \text{day}^{-1} \cdot \text{mole}^{-1}$, R = gas constant ($6.24 \cdot 10^4 \text{ cm}^3 \cdot \text{torr} \cdot \text{mole}^{-1} \cdot \text{K}^{-1}$) and T = absolute temperature ($^{\circ}\text{K}$).

Combining Eqs. (2) and (4) and for our experimental conditions ($T = 298^{\circ}\text{K}$; $D_{\text{H}_2\text{O}} = 0.280 \text{ cm}^2 \cdot \text{sec}^{-1}$; $\Delta P_{\text{H}_2\text{O}} = 23.76 \text{ torr}$) we obtain:

$$G_{\text{H}_2\text{O}} = 23.42 \frac{A_p}{L} \quad (5)$$

and substituting Eq. (3) into Eq. (5) we can express A_p and L as a function of egg weight:

$$\frac{A_p}{L} = 0.018 W^{0.780} \quad (6)$$

Equation (6) represents the geometrical factors of the shell that are responsible for the conductance of the shell as a function of the egg weight, namely, pore area and pore length. This relationship has broader implications since the same geometry determines the conductance for all gases which exchange across the shell.

THICKNESS OF THE EGG SHELL

On the basis of egg shell pore casts for many species of birds (Tyler 1956, 1964, 1966, 1969), we have assumed that the shell thickness is a convenient index of the pore length, L . From the data of Schönwetter (1960-71), we have plotted values of egg shell thickness and corresponding egg weight for 367 species (fig. 2) and calculated the regression:

$$L = 5.126 \cdot 10^{-3} \cdot W^{0.456} \quad (7)$$

The standard error of estimate for the log form of the function is ± 0.077 . The correlation coefficient is high ($r = 0.971$) and significant ($P < 0.001$).

TOTAL FUNCTIONAL PORE AREA

With the value of L as a function of egg weight we can now substitute Eq. (7) into Eq. (6) and obtain total functional pore area, A_p , as a function of the fresh egg weight:

$$A_p = 9.2 \cdot 10^{-5} \cdot W^{1.236} \quad (8)$$

Whether the increase in pore area with weight is achieved by increasing the number of pores or their diameter or some combination of the two is unknown and should be explored. We do know from Tyler that there seems to be

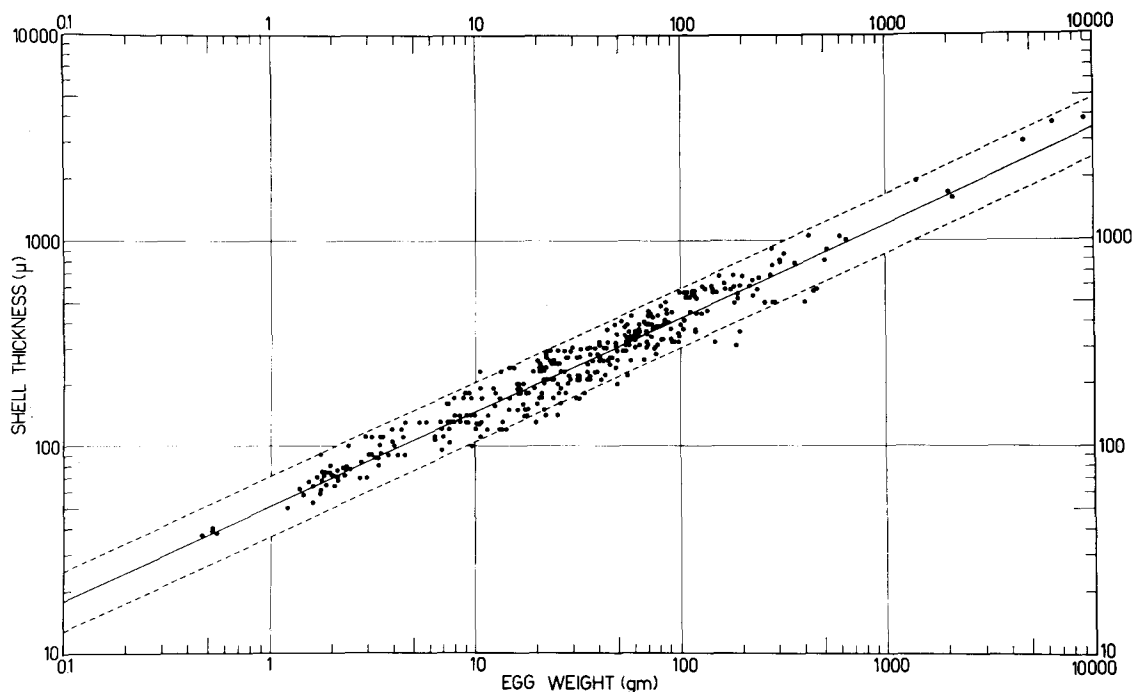


FIGURE 2. Regression of the egg shell thickness on egg weight. Values obtained from Schönwetter (1960-71), $n = 367$. Dotted lines enclose ± 2 standard errors of estimate and define the 95% confidence limits for the log of thickness.

a tendency of increasing complexity in pore structure with egg size. While Eq. (8) gives the general relationship of pore area as a function of weight, it is often desirable to calculate the pore area for a given egg on the basis of experimentally determined values of G_{H_2O} and L . For such calculations it is convenient to rearrange Eq. (5) to read:

$$Ap = 4.27 \cdot 10^{-4} \cdot G_{H_2O} \cdot L \quad (9)$$

where

Ap = the total functional pore area (mm²)

G_{H_2O} = the water conductance (mg · day⁻¹ · torr⁻¹)

L = shell thickness (μ).

RELATIONSHIP BETWEEN EGG WEIGHT, SHELL THICKNESS, CONDUCTANCE, AND TOTAL FUNCTIONAL PORE AREA

As shown above, we have established the following egg shell functions related to egg weight:

$$\begin{aligned} G_{H_2O} &= 0.432 \cdot W^{0.780} \\ L &= 5.126 \cdot 10^{-3} \cdot W^{0.456} \\ Ap &= 9.2 \cdot 10^{-5} \cdot W^{1.236} \end{aligned}$$

G_{H_2O} , L , and Ap can be plotted simultaneously as functions of egg weight as shown in figure 3. It should be pointed out that these relations

indicate only the behavior of best-fit values or the "ideal" egg and are useful in pointing out general relationships based on the laws of diffusion of gases. Nevertheless, they may serve as reference for the investigation of any particular species that deviates from these idealized relationships. For example, a typical chicken egg in our experiment has a weight of 53.85 g. The calculated pore area according to the general relationship for eggs of this size [Eq. (8)] is 1.23 mm². For hen's eggs we have obtained a G value of 14.36 mg · day⁻¹ · torr⁻¹ (table 1) and a shell thickness of 350 μ (Romanoff and Romanoff 1949). From Eq. (9), $Ap = 2.15$ mm², which agrees with the value calculated by Wangenstein et al. (1970-71), and is similar to anatomical observations (Romanoff and Romanoff 1949). The higher value obtained this way when compared with the "ideal" may indicate a certain selection pressure in hen's eggs toward increased functional pore area.

INTERPRETATION

We have shown that the conductance of water vapor across the egg shell increases with the egg weight raised to the 0.78 power. Since the transport of all gases (O₂, CO₂, H₂O) across the egg shell is by diffusion (Wangenstein et al. 1970-71; Wangenstein and Rahn 1970-71; Paganelli et al. 1971), the conduc-

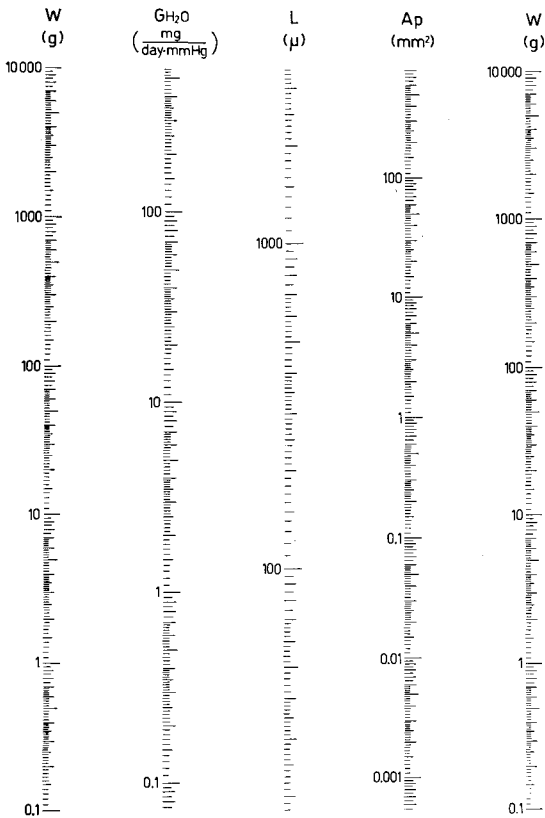


FIGURE 3. Simultaneous relationship between shell thickness (L), water vapor conductance (G), and total pore area (Ap) for given egg weights.

tance of an egg for any gas is proportional to its diffusion coefficient times the ratio of total pore area to shell thickness [Eq. (5)]. Thus the conductance for CO_2 and O_2 (G_{CO_2} and G_{O_2}) must also be proportional to $W^{0.78}$, a power function nearly identical with that describing the basal metabolic rate of adult birds and mammals as a function of their body weight. Since the water loss of an egg is independent of the metabolic rate, it is likely that the particular pore geometry which determines gas conductance evolved in response to the metabolic needs of the embryo, as pointed out by Wangenstein and Rahn (1970–71). Therefore the fact that $G_{\text{H}_2\text{O}}$ varies as $W^{0.78}$ is not surprising and merely reflects its dependence upon metabolic requirements.

The change of the pore geometry with egg size represents the optimization of two antagonistic properties, namely, the total pore area and the pore length. The difference between the power function for gas conductance, total pore area, and pore length is exemplified by comparing typical 1-g and 1000-g eggs.

In order to meet the increasing metabolic need which accompanies a 1000-fold increase in weight, gas conductance must increase 219

times ($\propto W^{0.78}$). However, the structural requirements of the egg shell demand a 23-fold increase in shell thickness ($\propto W^{0.456}$). Thus the total effective pore area must change by (219×23) or 5105 times, which is proportional to fresh egg weight raised to the sum of these two exponents, namely, 1.236.

SUMMARY

The rate of water loss from eggs per unit of water vapor tension difference is compared for 29 species. The water vapor conductance is proportional to the 0.78 power of the fresh egg weight. From values given in the literature, it can be shown that the thickness of the egg shell is proportional to the 0.456 power of the egg weight. On the basis of Fick's first law of diffusion, these two values allow one to compute the total functional pore area which is proportional to the fresh egg weight raised to the sum of these two exponents, namely, 1.236. It is the ratio of functional pore area to shell thickness which determines the conductance of all gases which exchange across the egg shell.

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